Genotypic and Environmental Effects on Grain Yield and Quality of Oat Grown in North Dakota

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ABSTRACT

The grain yield and quality determine much of the value of an oat (Avena sativa L.) crop to the producer. This study investigated effects of genotype and environment on grain yield and quality. Twelve oat genotypes were grown during 3 yr at four locations in North Dakota where detailed environmental data were being collected. Grain yield, test weight, groat percentage, groat weight, and groat composition (protein, oil, β-glucan, and starch concentrations) were evaluated. Results were subjected to analysis of variance and influences of environmental factors were evaluated by correlation analysis. Analysis of variance suggested that grain yield, groat starch, and ash concentrations were more strongly affected by environment than by genotype. Test weight, groat percentage, groat weight, protein, and β-glucan were about equally influenced by environment and by genotype, whereas groat lipid was more strongly influenced by genotype. Significant environment \times genotype interactions for all characteristics were attributed to differential resistance of genotypes to crown rust (caused by Puccinia coronata Corda var. aveneae W.P. Fraser & Ledingham) infection. Environments severely affected by crown rust produced grain with lower test weight, groat weight, and groat percentage in susceptible genotypes. Correlation analyses suggested that warm, bright (high solar radiation) spring weather, and cooler summer weather without excessive rains during grain filling generated the best oat yields with high quality grain.

Characteristics most commonly used to describe oat quality include test weight, groat percentage, groat weight, and groat composition. The major groat compositional characteristics relating to quality include the protein, oil, and β -glucan concentrations. Plant breeders strive to generate cultivars that will yield well and produce consistently high quality grain over a wide range of environments. A relatively small amount of information is available in the literature describing the effects of environment and genotype on oat grain yield and quality.

Test weight is the most commonly used method to evaluate oat quality (Forsberg and Reeves, 1992). Test weight is a measure of the density of oat grains as they are packed into a given volume. It is reported to be affected by kernel and groat size, groat density, hull thickness and length, and groat percentage as well as the presence of awns, diseases, and tertiary kernels (Murphy et al., 1940; Atkins, 1943; MacKey, 1959; Forsberg and Reeves, 1992). Several studies have reported genotype × environment interaction for oat test weight (Bartley and Weiss, 1951; Gullord and Aastveit, 1987).

Groat percentage is a measure of the proportion of

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Published in Crop Sci. 41:1066-1072 (2001).

the whole oat that is recovered as groat after dehulling. Groat percentage has long been recognized as an important indicator of oat quality (Love et al., 1925; Stoa et al., 1936; Atkins, 1943; Bartley and Weiss, 1951). Peek and Poehlman (1949) considered test weight to be a more valuable oat quality evaluation tool than groat percentage because hand-dehulling of oat was considered too tedious. Stoa et al. (1936) suggested that early maturing oat cultivars were superior in groat percentage, and rust susceptible lines were generally higher in percent hull. These conclusions were also supported by the findings of Bunch and Forsberg (1989). The studies of Bartley and Weiss (1951) indicated strong environmental effects on groat percentage and demonstrated positive correlations between groat percentage and yield, test weight and kernel weight. Youngs and Shands (1974) demonstrated that tertiary kernels had a higher groat percentage than primary and secondary kernels, although Palagyi (1983) found that genotypes with higher levels of tertiary kernels had lower groat percentage. He suggested that tertiary kernels compete with primary and secondary kernels for assimilate, preventing them from filling properly. Very little information is available concerning the control of oat groat weight, although one study (Gullord and Aastveit, 1987) indicated significant genotype × environment interactions for the trait.

Among the compositional components of oat, protein concentration often is ranked highly in importance because of its nutritional significance. Oat groats may contain from 124 to 244 g kg⁻¹ protein, and this protein is of higher nutritional quality than most other grains (Peterson, 1992). Studies have shown genotypic and environmental effects on oat protein concentration (Jenkins, 1969; Forsberg et al., 1974; Saastamoinen et al., 1989). In particular, nitrogen supply strongly affects oat protein concentration (Ohm, 1976; Welch and Yong, 1980; Welch et al., 1991; Humphreys et al., 1994; Jackson et al., 1994).

Oat contains much higher oil concentrations than do other small grains (Youngs, 1986). Higher oil content is an advantage for animal feeding because of its higher caloric content. However, in food applications, higher oil concentrations are deleterious because of their potential for rancidity and production of off-flavors. Studies have indicated that both genotype and environment affect groat oil concentration (Brown et al., 1966; Saastamoinen et al., 1989; Welch, 1975; Humphreys et al., 1994). Cooler growth environments have been reported to stimulate oil accumulation in groats (Beringer 1971, Saastamoinen et al., 1989). Negative correlations between protein concentration and oil concentration among different oat genotypes have been reported (Brown et al., 1966; Forsberg et al., 1974). This relationship has been disputed (Youngs and Forsberg, 1979), and cultivars with both high protein and oil concentrations have been developed.

The β -glucan component of oat has garnered increasing interest in recent years because of studies that indicated that β -glucans associated with oat bran in diets can lower blood cholesterol in both animals and humans (Peterson, 1992). Variation in groat β -glucan concentration among different oat genotypes and differing environmental conditions have been studied (Welch and Lloyd, 1989; Peterson, 1991; Welch et al., 1991; Brunner and Freed, 1994; Humphreys et al., 1994; Jackson et al., 1994; Peterson et al., 1995).

Although strong genotypic differences in β-glucans can be demonstrated consistently, environmental effects have been more difficult to document (Peterson, 1991; Peterson et al., 1995). For example, of three recent studies where the effects of nitrogen fertilization on β -glucan accumulation were examined, one study reported significant nitrogen × location and nitrogen × year interactions affecting β-glucan concentration in groats, whereas, the other two studies found no significant main effect or interaction effects of nitrogen on β-glucan concentration (Brunner and Freed, 1994; Humphreys et al., 1994; Jackson et al., 1994). Several studies have suggested that drought conditions may influence β-glucan accumulation in oat (Peterson, 1991; Welch et al., 1991; Brunner and Freed, 1994; Peterson et al., 1995), but no study has conclusively demonstrated this.

Starch is the major storage component in oat. However, because most of the value of oat lies in the nonstarch components, its concentration is usually not considered in quality analyses. The remaining components of oat composition include ash and fiber components other than β-glucans. Fiber components, which include pentosans (arabinoxylans), cellulose, lignin, and galactomannans (Aspinall and Carpenter, 1984; Henry, 1987) are important to quality because of their contribution toward total dietary fiber. Ash represents the mineral components of oat and is primarily composed of phosphorus, calcium, potassium, copper, manganese, iron, sodium, and magnesium (Peterson et al., 1975). Although many of these are considered essential minerals to be included in the diet, they are generally not considered in selection of oat for quality.

In this study, 12 oat genotypes adapted for production in North Dakota and divergent in protein, oil, β -glucan, and groat size were grown at four different locations

over three years. Detailed environmental data were gathered at these sites. Our goals were to determine the relative effects of specific meteorological factors on oat grain yield and quality, and to determine sources of quality trait variation observed in the oat breeding program.

MATERIALS AND METHODS

Plant Material

Ten oat cultivars (AC Marie, Bay, Hazel, Hytest, Jerry, Marion, Paul, Riel, Robert, and Whitestone, and two breeding lines, ND880786, and ND880946) were grown in 1994, 1995, and 1996 at Carrington, Edgeley, Minot and Prosper, ND, USA. The soil type at Carrington is Heindahl (coarse, loamy, mixed Udic Haploborolls) and Emrick loams (coarse, loamy, Pachie Haploborolls). Soils at Edgeley are Barnes (fine-loamy, mixed Udic Haploboroll) and Cresbard (fine, Montmorillonitic Glossic Udic Natriboroll) loam complex. Soils at Minot are Williams (fine, loamy, mixed Typic Argiborolls) loam. Soils at Prosper are Perella (fine, silty, mixed, frigid, Typic Haploquolls) and Beardon (fine, silty, mixed frigid, Aeric Calciaquolls) silty clay loams.

A seeding rate of 2.47×10^6 kernels ha⁻¹ was used for all experiments. Herbicide treatments consisted of pre-emergence application of 3.93 kg ha⁻¹ propaclor (2-chloro-*N*-isopropylacetanilide) and post-emergence application at the 3-leaf stage with a tank mix of 0.14 kg ha⁻¹ thifensulfuron {methyl 3 [[[(4-methoxy-6-methyl-1,3,5-triazin-2yl)amino]carbonyl] amino]sulfonyl]-2-thiophenecarboxylate}, 0.07 kg ha⁻¹ tribenuron {methyl 2-[[[[N-(methoxy-6-methyl-1,3,5-triazin-2yl) methylamino] carbonyl] amino] sulfonyl] benzoate}, and 0.14 kg ha⁻¹ clopyralid (3,6-dichloro-2-pyridinecarboxylic acid, monoethanolamine salt). Experimental units consisted of four rows spaced 0.3 m apart and 2.4 m long. The two center rows were harvested with a two-row binder and threshed with a plot thresher. Seed was cleaned with an air screen cleaner to remove chaff. Test weight was determined by weighing a fixed volume of grain. Planting and harvest dates are shown in Table 1.

Climatic data included daily high and low temperatures, precipitation, and solar radiation. Climatic data were gathered by automated stations maintained by the Soil Science Department, North Dakota State University, Fargo, ND. Seasonal means of climatic conditions for each environment analyzed here are presented in Table 1.

Sample Preparation

Sound grain was stored in paper bags and envelopes. Whole oat samples were steam-treated in a vegetable steamer for

Table 1. Planting and harvest dates and mean seasonal climatic data for the environments evaluated in this study.

Location	Year	Planting date	Harvest date	Mean daily solar radiation	Mean daily high temperature	Mean daily low temperature	Total seasonal precipitation
				Langley	°	C	cm
Carrington	1994	4 May	8 Aug	511	21.1	7.9	22.3
Carrington	1995	5 May	14 Aug	488	20.3	8.3	33.6
Carrington	1996	3 May	8 Aug	488	19.7	6.8	28.1
Edgeley	1994	12 May	8 Aug	517	21.9	8.7	28.5
Edgeley	1995	23 May	22 Aug	485	20.8	9.1	29.4
Edgeley	1996	23 May	21 Aug	511	20.7	8.0	21.7
Minot	1994	20 Apr	11 Aug	513	21.4	8.2	30.5
Minot	1995	3 May	14 Aug	474	20.8	8.3	26.3
Minot	1996	2 May	20 Aug	479	20.6	7.8	18.6
Prosper	1994	9 May	4 Aug	493	22.3	9.0	33.1
Prosper	1995	24 May	15 Aug	465	21.7	9.3	29.3
Prosper	1996	28 May	20 Aug	492	21.1	8.4	17.3

Genotype	Yield	Test weight	% Groat	Groat weight	Groat starch	Groat protein	Groat lipid	Groat β-glucan	Groat ash
	Mg ha ⁻¹	$kg m^{-3}$	%	mg			g kg ⁻¹ dry bas	sis —	
AC Marie	3.41	433	68.8	20.2	596	146	78.1	48.8	18.7
Bay	4.11	457	66.1	19.5	590	196	46.4	51.9	20.4
Hazel	3.49	493	70.8	21.8	571	191	69.9	53.3	21.3
Hytest	3.31	546	71.2	23.3	571	195	54.2	51.6	20.7
Jerry	3.63	512	68.9	21.1	598	173	50.0	43.4	19.6
Marion	3.62	477	67.8	22.4	581	165	65.6	57. 6	20.3
ND880786	3.14	457	64.0	16.8	591	161	68.7	57.0	19.8
ND880946	3.94	466	68.9	18.7	598	158	67.2	53.3	18.6
Paul†	3.22	601	91.7	21.3	572	183	71.7	49.9	19.1
Riel	3.85	504	70.7	20.9	592	175	59.5	46.3	18.4
Robert	3.51	468	67.7	22.5	604	157	59.9	43.3	19.1
Whitestone	3.85	470	63.7	17.0	602	160	63.1	47.7	18.7
LSD‡ (0.05)	0.46	20	2.7	1.2	12	5	1.4	2.0	0.6

Table 2. Genotypic means of oat grain yield and grain quality characteristics across 12 environments.

20 min to inactivate enzymes. Samples were dehulled with a Codema Laboratory Oat Huller (Codema Inc., Eden Prairie, MN)¹. The groat proportion was obtained by weighing the sample before and after dehulling. Dehulled groats were cleaned by hand to ensure that all hulls and broken groats were removed. Oil concentration and groat weight were determined on whole groats. Groats for starch, protein, β -glucan, and ash analyses were milled in a Retsch model ZM-1 centrifugal mill with a 0.5-mm collar screen (Brinkmann Instruments, Westbury, NY). Flour was stored in small sealable plastic bags and placed in a desiccator at room temperature until analyzed.

Chemical Analyses

Moisture of flour samples was determined by heating a 2-g flour sample for 2 h in a convection oven at 130°C. Samples were allowed to cool in a desiccator and reweighed. Moisture was proportional to the weight loss during the heat treatment. All chemical analyses are expressed on a dry weight basis.

Oil analysis was performed on whole groats with an Oxford 4000 NMR (Abingdon, England). Groats were dried in a convection oven at 130°C for 2 h to eliminate the interference of water to the oil signal. Samples were allowed to cool in a desiccator before analysis. Calibration of the instrument had been established by comparison of signals with groats with known oil concentration, established by Soxhlet extraction with petroleum ether. Starch was analyzed according to the American Association of Cereal Chemists (1995) method 76-11

Protein was analyzed by combustion analysis with a Leco FP-428 Nitrogen Analyzer (Leco Corporation, St. Joseph, MI). Total nitrogen was converted to protein by multiplying by 6.25.

Ash of a 2-g sample was determined in an ashing oven by initially incubating samples in crucibles for 1-h at 350°C, then increasing the oven temperature to 450°C, and 590°C after 1-h intervals, then maintaining 590°C for 18 h. After ashing, crucibles were removed from the ashing oven and allowed to cool in a desiccator before measuring ash weight. Total (1 \rightarrow 3), (1 \rightarrow 4)- β -D-glucan (β -glucan) was determined by the method of McCleary and Glennie-Holmes (1985).

Groat weight was derived from the number of kernels in a 10-g sample.

Experimental Design and Statistical Analyses

Experimental plots were arranged in a randomized complete block design with three replicates within each environ-

ment. Analysis of variance was performed with the SAS General Linear Model procedure (SAS Institute, Cary, NC), where all environments were considered random and genotypes were considered fixed. Pearson correlation matrixes were calculated across all environments for each genotype with the Statistix computer package (Analytical Software, Tallahassee, FL) and were pooled and their homogeneity determined by procedures described by Steel et al. (1997, p. 295–297). Significance of individual correlation coefficients were evaluated using 108 degrees of freedom, according to Steel et al (1997, p. 295).

RESULTS AND DISCUSSION Means and ANOVA

Genotypic means of grain yield and quality characteristics (Table 2) indicated that the hull-less cultivar Paul ranked highest in groat proportion and test weight and was second lowest in grain yield, as would be expected for a hull-less cultivar. Calculation of groat yields (not shown) indicated that Paul had the highest groat yield of all the cultivars grown.

Environmental means for grain yield and quality characteristics (Table 3) indicated that the Carrington, Edgeley, and Prosper locations in the 1995 growing year had reduced grain yields, test weights, groat percentages, and groat weights compared to other environments. These differences are attributed to particularly severe crown rust infections at those locations in that year. Unfortunately, no quantitative measures of crown rust infestation of plots were collected during this experiment. Groat composition appeared to be relatively unaffected at the locations heavily infested by crown rust (Table 3).

Analyses of variance indicated significant genotype \times environment interactions (P < 0.05) for all characteristics measured (Table 4), although the magnitude of the interactions MS were relatively small in comparison to the main effects. Interactions for yield, test weight, groat percentage, and groat weight were all due to differences in ranking as well as differences in magnitude of changes of genotypes among the environments. The most likely factor contributing to the significant environment \times genotype interactions for yield, test weight, groat percentage, and groat weight was the differential level of crown rust infection among the cultivars. The genotypes

[†] Hull-less genotype

 $[\]ddagger$ Calculated using the environment \times genotype mean square as an error term.

¹The mention of firm names or trade products does not imply that they are endorsed or recommended by the U.S. Department of Agriculture over other firms or similar products not mentioned.

Table 3. Environmental means of oat grain yield and grain quality characteristics across 12 environments.

Environment	Yield	Test weight	% Groat	Groat weight	Groat starch	Groat protein	Groat lipid	Groat β-glucan	Groat ash
	Mg ha ⁻¹	kg m ⁻³	%	mg			— g kg ⁻¹ —		
Carrington '94	4.31	508	80.3	19.7	594	163	61.7	53.9	20.9
Carrington '95	1.79	408	57.5	15.9	614	162	63.6	52.1	22.1
Carrington '96	1.90	468	63.6	21.6	549	166	63.4	47.2	19.1
Edgeley '94	4.52	541	77.2	23.2	640	180	58.7	55.5	19.4
Edgeley '95	3.09	415	64.6	15.5	622	153	68.6	53.5	21.1
Edgeley '96	5.23	520	66.1	25.3	547	186	61.7	45.6	17.5
Minot '94	4.77	570	82.4	22.7	597	189	61.5	51.2	17.1
Minot '95	2.78	547	74.4	22.7	600	190	65.0	49.3	18.3
Minot '96	3.40	538	67.3	23.3	546	184	63.6	44.7	16.0
Prosper '94	4.19	493	81.7	19.9	588	168	57.3	52.1	22.5
Prosper '95	2.60	411	63.6	16.9	620	161	63.4	52.8	22.6
Prosper '96	4.49	467	61.5	18.9	548	158	65.9	46.3	18.2
LSD [†] (0.05)	0.21	12	1.3	0.9	24	4	1.7	3.2	0.8

 $[\]dagger$ Calculated with the environment imes replicate mean square as the error term.

Paul and Bay appeared to be more resistant to crown rust races prevalent that year because these genotypes were less severely affected than were the other genotypes. The significant (P < 0.05) genotype \times environment interactions for groat composition were almost entirely due to differences in changes in magnitude of values among the genotypes in the different environments. The genotypic ranking for compositional characters was very uniform among the environments.

The magnitude of the main effect MS (Table 4) suggested that yield, groat starch and groat ash were more strongly influenced by environment than genotype. Test weight, groat percentage, groat weight, protein, and β -glucan appeared to be about equally affected by environment and genotype, whereas groat lipid appeared to be more strongly influenced by genotype than by environment.

Correlation Analyses

Phenotypic correlations of oat grain yields and quality characteristics with environmental conditions were calculated to determine environmental conditions associated with oat characteristics (Table 5). Grain yield was correlated positively with both high and low temperatures in April and May, indicating that warm spring weather was favorable for higher yields. These conditions provided for earlier planting and accelerated seedling development. Both July and August low temperatures were correlated negatively with yield. This suggested that the high night temperatures during the final stages of grain development may reduce grain yields through excessive respiration. Several previous studies have found

negative relationships between high night temperatures and grain yield in maize and other crops (Peters et al., 1971; Christy and Williamson, 1985). They suggested that excessive respiration at night depleted photosynthate that would have otherwise contributed to grain yield. A negative correlation between seasonal precipitation and grain yield (Table 5) suggested that most of the environments had adequate moisture to sustain growth. Excessive rain in July probably contributed to more severe crown rust infections, which were associated with negative effects on yields. Seasonal solar radiation was highly and correlated positively with yield (Table 5). The importance of solar radiation to yield suggests that gross photosynthesis may have been a major limiting factor to plant growth. Many previous investigators have attempted to link photosynthesis and yield, and most have failed (Gifford et al., 1984), usually because so many factors influence yield. However, shading experiments have resulted in decreased yields in maize, Zea mays L., (Early et al., 1967; Reed et al., 1988) and in soybeans, Glycine max (L.) Merr., (Christy and Porter, 1982). In soybeans, 50% shade resulted in a 25 to 35% yield decrease (Christy and Porter, 1982).

Test weight and groat percentage, like yield, were correlated positively with warm spring temperatures and correlated negatively with hot late summer temperatures (Table 5). It is likely that test weight and groat percentage were affected by many of the same physiological processes discussed that affected yield. Like yield, test weight was also correlated negatively with July precipitation. This probably also was due to the association of crown rust infections with heavy July pre-

Table 4. Mean squares (MS) for grain yield and quality characteristics of 12 genotypes across 12 environments.

Source	df	Grain yield, MS	Test weight, MS	% Groat, MS	Groat weight, MS	
Environment	11	48.07**	115 104**	2 713.8**	366.6**	
Replicate (Environment)	24	0.19	616	7.2	3.6	
Genotype	11	3.24**	76 366**	1 900.9**	157.2**	
Genotype × Environment	121	0.95**	1 895**	32.5**	6.9**	
Residual	264	0.15	229	8.9	1.1	
Source	df	Starch, MS	Protein, MS	Lipid, MS	β-glucan, MS	Ash, MS
Environment	11	40 777**	6 296**	334**	469.2**	180.5**
Replicate (Environment)	24	2 486	72	13	42.6	2.7
Genotype	11	5 498**	9 946**	3 120**	791.5**	31.9**
Genotype × Environment	121	695**	103**	9**	18.0**	1.6**
Residual	264	398	24	2	13.1	0.4

^{**} *P* < 0.01.

Table 5. Phenotypic correlations of grain yield and grain quality characteristics with environmental condition across twelve environments pooled from 12 genotypes.

	Yield	Test weight	% Groat	Groat weight	Groat starch	Groat protein	Groat lipid	β-Glucan	Groat ash
				Mean I	Daily High Temp	perature			
Season	0.494**	0.180	0.580**	-0.073	0.425**	0.042	-0.542**	0.449**	0.308**
April	0.591**	0.476**	0.843**	0.201*	0.414**	0.230*	-0.696**	0.517**	0.168
May	0.422**	0.364**	0.830**	0.070	0.467**	0.093	-0.703**	0.586**	0.310**
June	-0.186	-0.564**	-0.495**	-0.368**	0.082	-0.385**	0.167	-0.016	0.391**
July	-0.040	-0.266**	-0.052	-0.452**	0.383**	-0.149	0.352**	0.228*	0.244*
August	-0.323**	-0.364**	-0.702**	-0.181	-0.291*	-0.092	0.707**	-0.466**	-0.466**
				Mean I	Daily Low Temp	perature			
Season	0.160	-0.027	0.413**	-0.138	0.092	-0.119	-0.519**	0.205*	0.463**
April	0.493**	-0.055	0.405**	-0.267*	0.613**	-0.206*	-0.321**	0.627**	0.477**
May	0.536**	0.153	0.618**	-0.141	0.563**	-0.042	-0.441**	0.586**	0.382**
June	-0.168	-0.390**	-0.044	-0.449**	0.586**	-0.209*	0.062	0.430**	0.593**
July	-0.427**	-0.353**	-0.206*	-0.501**	0.451**	-0.114	0.380**	0.219*	0.278*
August	-0.533**	-0.517**	-0.593**	-0.365**	0.126	-0.136	0.539**	-0.111	0.137
					Precipitation				
Season	-0.362**	-0.283**	0.175	-0.377**	0.623**	-0.133	-0.259*	0.565**	0.624**
April	-0.198*	-0.143	-0.105	-0.183	0.705**	-0.033	0.087	0.478**	0.188
May	0.134	-0.081	-0.294**	0.014	-0.122	0.080	0.498**	-0.205	-0.290*
June	0.220*	0.570**	0.568**	0.272*	-0.225*	0.381**	-0.242*	-0.106	-0.356**
July	-0.498**	-0.527**	-0.122	-0.439**	0.362**	-0.427**	-0.315**	0.400**	0.744**
August	-0.063	0.109	0.529**	-0.109	0.656**	0.148	-0.406**	0.568**	0.467**
_				Mean	Daily Solar Rad	diation			
Season	0.668**	0.480**	0.487**	0.407**	0.019	0.232*	-0.472*	0.170	-0.226*
April	0.579**	0.522**	0.649**	0.442**	-0.040	0.195	-0.660**	0.192	-0.129
May	0.344**	0.400**	0.804**	0.085	0.470**	0.071	-0.590**	0.591**	0.204*
June	-0.049	-0.189	-0.531**	0.214*	-0.358**	-0.033	0.272	-0.389**	-0.212*
July	-0.085	0.261*	0.077	0.102	0.386**	0.405**	0.261*	0.141	-0.338**
August	-0.297**	-0.054	-0.643**	0.311**	-0.542**	0.217*	0.408**	-0.662**	-0.503**

^{*} Indicates significance at P = 0.05.

cipitation. Test weight and groat percentages were correlated positively with June precipitation, suggesting the importance of good vegetative growth towards full groat development. Test weight and groat percentages were also correlated positively with seasonal solar radiation, again suggesting the importance of gross photosynthesis to the grain filling process. The similarity of factors affecting both test weight and groat percentage is consistent with previous studies indicating correlations between test weight and groat percentage (Doehlert et al., 1999).

Groat weight differed from yield, test weight and groat percentage, in that it was less strongly correlated with warmer spring temperatures, but was more strongly negatively correlated with warmer summer temperatures. This suggested that groat weight was more strongly influenced by temperatures occurring during the grain filling period.

Groat starch was correlated positively with warmer

temperatures in most months (Table 5). It was also correlated positively with precipitation for the season, and for April and August. Physiological reasons for mechanisms by which these environmental factors would affect groat starch are not clear at this time.

Groat protein was significantly correlated with relatively few environmental factors (Table 5). Of particular interest was a positive correlation with June precipitation and a negative correlation with July precipitation. June precipitation may have stimulated vegetative growth that allowed oat plants to accumulate nitrogen prior to grain filling, and July precipitation may have washed any remaining soil nitrogen out of the root zone, preventing its accumulation in grain. Alternatively, July precipitation may have stimulated starch accumulation, which would have diluted the protein concentration.

Groat lipid concentration was correlated negatively with warm spring temperatures but correlated positively with warmer summer temperatures. This might appear

Table 6. Phenotypic correlations of oat grain yield, quality characteristics and composition with each other calculated across 12 environments. Correlation coefficients are pooled from 12 genotypes.

	Yield	Test weight	Groat percentage	Groat weight	Groat lipid	Groat ash	Groat protein	Groat starch
Test Weight	NH†							
Groat Percentage	0.525**	0.680						
Groat Weight	NH	NH	NH					
Groat Lipid	-0.344**	-0.451**	-0.587**	-0.414**				
Groat Ash	-0.377**	-0.632**	-0.064**	-0.708**	-0.158			
Groat Protein	NH	NH	0.407**	0.803**	-0.338*	-0.608**		
Groat Starch	-0.099	-0.182	0.225*	-0.381**	-0.101	0.513**	-0.153	
Groat β-glucan	-0.067	-0.202*	0.343**	NH	NH	0.615**	NH	0.729**

^{*} Indicates significance at P = 0.05.

^{**} Indicates significance at P = 0.01.

^{**} Indicates significance at P = 0.01.

[†] NH = correlations coefficients not homogenous across genotypes.

to be inconsistent with earlier studies that suggested that cooler temperatures during grain fill increased oil accumulation (Beringer, 1971; Saastamoinen et al., 1989). It should be noted that very little overall variation in groat oil concentration could be attributed to the environment, and that genotypic effects accounted for most of the variation (Table 4).

Groat β -glucan concentration was correlated with many of the same environmental factors as groat starch (Table 5). This suggests that these two complex polymers of glucose responded in about the same way to environmental conditions. Several earlier studies had suggested that drought conditions might stimulate β -glucan concentrations in oat groats (Peterson, 1991; Welch et al., 1991; Brunner and Freed, 1994; Peterson et al., 1995). In the current study, precipitation in July and August was correlated positively with β -glucan concentration, suggesting the opposite to these previous studies.

Groat ash concentration was correlated positively with warmer temperatures in most months and with precipitation in July and August. Physiological reasons for these correlations are not clear.

Attempts to correlate quality characteristics with each other across environments were partially unsuccessful because of excessive heterogeneity of correlation coefficients among genotypes (Table 6). However, it was apparent that groat percentage was correlated positively with yield and test weight. This suggests that conditions leading to higher yields generally also lead to improved quality. This analysis also indicated that across environments, starch concentration was correlated positively with ash and β -glucan concentration, protein concentration was correlated positively with groat weight, and lipid concentration was correlated negatively with yield, test weight and groat percentage and weight.

In summary, it appears that warm spring weather with abundant sunlight were most conducive to improved oat grain yield and quality. Also, conditions in midsummer that discouraged disease development, such as cooler temperature and less than excessive rains, were associated with improved yields and grain quality. Relatively low environmental effects on the economically important compositional traits of protein, lipid and β -glucan indicate excellent potential for trait stability across environments.

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Diallel Analysis for Tocopherol Contents in Seeds of Rapeseed

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ABSTRACT

Because of their nutritional and antioxidative properties, tocopherol production is an interesting trait for the lipid quality of oil crops. Total tocopherol content in rapeseed (Brassica napus L.) is medium to low, and therefore, higher levels of tocopherol are desirable in this species. The objective of the present study was to determine the inheritance of α -, γ -, and total tocopherol content and the α -/ γ tocopherol ratio in seed of rapeseed. Two diallel mating designs with six parents each were used. In Diallel I, the parents selected were high or low for total tocopherol content and in Diallel II, the parents were high or low for the $\alpha\text{-/}\gamma\text{-tocopherol}$ ratio. Parents and F_1 hybrids were tested in a screenhouse in 1998 and under field conditions in 1999 by means of a completely randomized design with two replications. In addition, 10 selected F₂ populations were grown along with their respective parents. Compared with the parents, the F₁ hybrids showed a significantly higher γ -tocopherol content of about 6 mg kg $^{-1}$ seed for Diallel I and 24 mg kg⁻¹ seed for Diallel II. General combining ability effects in both diallels were highly significant (P < 0.01) and much larger than specific combining ability effects for all traits studied. Reciprocal effects were not statistically significant. γ-Tocopherol was not correlated with α -tocopherol. The results indicate that tocopherol content and composition inheritances are strongly associated with additive gene action in rapeseed.

An important group of natural antioxidants with biological activity in vegetable oils is the tocopherols. They occur in four derivatives $(\alpha$ -, β -, γ -, and δ -tocopherol, the α -form is known as vitamin E), differing in the methylation of the tocol head group (Larson, 1988). The main biochemical function of the tocopherols is believed to be the protection of polyunsaturated fatty acids against peroxidation (Kamal-Eldin and Appelqvist, 1996). The vitamin effectiveness of the tocopherols is very different, with α -tocopherol being the most effective among all tocopherol derivatives. However, as antioxidant in vitro, the γ -tocopherol derivative is the most

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Published in Crop Sci. 41:1072-1079 (2001).

efficient of the fours with the α -form being the least effective (Pongracz et al., 1995).

In rapeseed, total tocopherol content ranges from 300 to 800 mg kg $^{-1}$ oil (Appelqvist, 1972; Goffman and Becker, 1998). These values are medium to low compared with those of other oil plants. Rapeseed oil contains, on average, 64% γ -tocopherol, 35% α -tocopherol, and a very low percentage (<1%) of δ -tocopherol (Appelqvist, 1972; Goffman and Becker, 1998). The ratio of the content of α - to γ -tocopherol can be used to describe the tocopherol composition in rapeseed. Goffman and Becker (1998) found this ratio varied from 0.32 to 1.40. Since γ -tocopherol exerts lower biological activity than does α -tocopherol by ten-fold (Pongracz et al., 1995), an increase in the α -tocopherol fraction could improve the antioxidant and vitamin activities.

To capitalize on the positive effect of tocopherols in rapeseed breeding programs, investigation of the genetic control of these compounds is required. The genetics of tocopherols was investigated in sunflower (*Helianthus annuus* L.) seeds by Demurin (1993), where two nonallelic genes controlling the tocopherol composition were identified. In oilseed rape, the genetic control of tocopherols is unknown. The objective of the present study was to determine the inheritance of α -, γ -, and total tocopherol contents and the α -/ γ -tocopherol ratio in seeds of rapeseed.

MATERIALS AND METHODS

In 1997, two complete diallel crosses including reciprocals were produced using two sets of six genotypes each. In the first diallel (Diallel I), the parents selected were high or low for total tocopherol contents and in the second diallel (Diallel II), the parents were high or low for the α -/ γ -tocopherol ratio (Table 1). The hybrid seed was produced by hand pollination, and each diallel cross was carried out twice with two independent pairs of parental plants. The progenies of these two independent crosses were treated separately as replications in the screenhouse and field experiments. In 1998, the parental lines and the resulting F_1 plants of the two diallels were tested in

Abbreviations: GCA, general combining ability; λ_{ex} , excitation wavelength; λ_{em} , emission wavelength; MAT, maternal effect; NONM, nonmaternal effect; REC, reciprocal effect; SCA, specific combining ability; SD, standard deviation; total-T, total tocopherol content.